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ORIGINAL ARTICLE

Polyploidy, alien species and invasiveness in Polish angiosperms

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Abstract Chromosome numbers, mainly for Polish flora, were examined in order to investigate whether such features as chromosome numbers and polyploid frequencies are correlated with a plant's origin (native vs. alien) and invasiveness. Polyploid frequencies were estimated using three methods: the 11 and 14 thresholds and the 3.5 *x* value. Comparisons of the 2*n* values were done on different levels: in all angiosperms and in dicots and monocots separately. Invasive and non-invasive plants were compared in the entire dataset and in alien species only. Significant differences in both chromosome numbers and polyploid frequencies between alien and native species were observed. In most cases, native plants had more chromosomes and were more abundant in polyploids than in alien species. Also, monocots had higher polyploid frequencies than dicots. Comparisons of invasive and non-invasive plants done for all of the data and only for alien species showed that invasive species generally had more chromosomes and polyploids were more frequent in them than in the latter group; however, these differences were not always statistically significant. Possible explanations for these observations are discussed.

Keywords Invasiveness · Alien species · Chromosomes · Polyploidy · Evolution · Plants

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Introduction

Polyploidy is usually defined as the occurrence of more than two genomes in a nucleus. Polyploid organisms (polyploids) are formed as a result of polyploidization, which is believed to play a crucial role in plant evolution. The two main types of this process are: autopolyploidization, in which the multiplied genomes belong to the same species; and allopolyploidization, in which an increase in the number of genomes is accompanied by hybridization.

The estimated fraction of polyploids or their descendants ranges from 30 to 80 % in about 250,000 species of angiosperms (Bennett 2004). Such a wide range of approximation is the result of the different methods and criteria that have been used in assigning taxa to diploids or polyploids. Because polyploidization involves the multiplication of genomes, the easiest way to detect polyploids seems to be to set a threshold of a given number of chromosomes as the level above which a taxon is regarded as polyploid. Such a method is especially useful when it is used for large sets of data—the only criterion needed is the chromosome number. Naturally, the result obtained depends entirely on the threshold value that is applied. The most well-known estimations are $n \geq 11$, proposed by Goldblatt (1980) and $n \geq 14$, proposed by Grant (1981). Wood et al. (2009), in their studies on the frequency of polyploid speciation, proposed a modified threshold method: species should be regarded as polyploid if the somatic chromosome number is greater than or equal to 3.5 times the lowest haploid count of the host genus.

A method based on knowing the *x* (basal set of chromosomes) of taxa was recently used to estimate the polyploid fraction in Polish angiosperms, which were comparable to the thresholds proposed by Goldblatt, Grant and Wood (Gacek et al. 2011). While the scores obtained

using the threshold methods gave polyploid frequencies at levels of 64.64, 50.89 and 42.89 %, respectively, calculations that were based on the generic basic chromosome numbers showed 49.45 % of polyploids and 4.11 % of diploid/polyploid cytotypes.

More in-depth studies, including molecular analysis, have revealed that some species, which due to their low chromosome number are regarded as diploids, have a polyploid origin. One of the most well-known examples is maize. However, its chromosome number ($n = 10$) is below even Goldblatt's threshold, its molecular data has proved its tetraploid origin (Gaut and Doebley 1997). Even the genome of *Arabidopsis thaliana*, which is known for its small genome ($\sim$157 Mb) (Bennett et al. 2003) and chromosome number ($2n = 10$), might have been duplicated two to three times in the past (Vision et al. 2000; Bowers et al. 2003). A recent analysis of genomic studies revealed that almost all angiosperms have polyploid ancestors, and therefore, according to some authors, the question "What proportion of angiosperms are polyploid?" should be replaced with "How many episodes of polyploidy characterize any given lineage?" (Soltis et al. 2005, 2009).

The discrepancies between the molecular data and the "conventional" methods mentioned above are mainly caused by the changes in genomes that occurred after the polyploidization, including the rearrangements and loss of chromosomes that result in comparatively low chromosome numbers. In light of these results, estimations of polyploid frequencies based on conventional methods should be treated as frequencies of "recently" formed polyploids. However, although they may not reveal the real number of taxa that ever had a polyploidization event in their evolutionary history, they may be useful in other types of studies, including research on the influence of polyploidization on given features such as invasiveness.

Regardless of the method used in estimating polyploid frequency, there is no doubt that polyploidy plays a crucial role in the evolution of angiosperms, and therefore, many studies are focused on this subject. One of the most interesting questions about polyploidy is whether the multiplication of the genomes offers any evolutionary advantages. Authors usually mention such factors as the masking of deleterious mutations, a reduction in the "inbreeding depression effect", fixed heterozygosity, heterosis, additivity in gene expression, nuclear–cytoplasm interactions and an enhanced phenotype, e.g., larger cells and organs (Ronfort 1999; Otto and Whitton 2000; Soltis and Soltis 2000; Levin 2002; Wang et al. 2006; Otto 2007; te Beest et al. 2012).

Invasive plants are generally regarded as alien species that, after passing a series of transitional stages, escape into the wild and form a stable population there, eventually reaching the phase of uncontrolled spreading and becoming a problem (Richardson and Pyšek 2006; Williamson 2006; Pyšek et al. 2008). Therefore, the preconditions for a species to be defined as invasive must include the stage of their naturalization. Understanding the features that influence a plant's ability to be naturalized in a new ecosystem may be crucial for understanding the phenomenon of invasiveness. Features that are regarded as evolutionarily beneficial may be responsible for a plant's ability to colonize new areas and eventually become invasive; thus, a question that naturally arose was whether polyploidization or just an increase in genome size supports such capabilities. This subject is not only interesting but also significant practically. Invasions of alien species are currently perceived as one of the most serious threats to global biodiversity (Tokarska-Guzik et al. 2011). Although some studies have focused on searching for a correlation between these phenomena in selected taxa, the subject has not yet been well explored (Hull-Sanders et al. 2009).

The influence of polyploidy on a single species, *Centaurea maculosa* (syn. *C. stoebe*), was studied by Treier et al. (2009), who analyzed the ploidy level in 93 native and 48 invasive populations. In Europe, where it originates, populations were dominated by diploids, whereas in North America, where it was introduced in the late nineteenth century and became a highly invasive plant, tetraploids were much more frequent and diploids were found only in mixed populations. These results were later partially contested by authors who did not find diploids in this area and suggested that the polyploidy of N American populations may be caused by their origin rather than as the result of selection (Mráz et al. 2012; Thebault et al. 2011). Ambiguous results were also obtained by Hull-Sanders et al. (2009), who investigated the occurrence of diploid, tetraploid and hexaploid cytotypes of *Solidago gigantea* in its native range in the USA and its introduced range in Europe. Tetraploids were the most common in both ranges, but were more dominant in Europe. Hexaploids, however, were the most geographically restricted and were found in only two populations in the United States.

Lowry and Lester (2006) studied 60 taxa in the genus *Clarkia* in Western North America and showed that polyploid species have a significantly larger range size than diploids. Simultaneous studies on the flora of Singapore, which is regarded as a global hotspot for invasive species, proved that all of the highly invasive plants investigated on this area were polyploids (Pandit et al. 2006). Pandit et al. (2011) not only compared invasive with non-invasive plants, but also included endangered species in their studies. They collected worldwide data on the chromosome numbers for 640 endangered species and their 9,005 congeners and for 81 invasive species and their 2,356 congeners. Data analysis showed that while endangered

plants are usually diploids, invasive plants have more chromosomes and they are more likely to be polyploids. Recently, the role of polyploidy in plant invasions was also reviewed by te Beest et al. (2012).

An interesting approach to the subject was presented recently by Kubešová et al. (2010) who compared the genome size of naturalized and native species in the Czech Republic. The authors also compared the genomes of invasive species with non-invasive but alien species. Genome sizes were determined using the flow cytometry technique, and therefore DNA amounts, not chromosome numbers, were analyzed. These studies resulted in the conclusion that naturalized species generally had smaller genomes than their native congeners. These observations correspond with the idea that small genomes favor invasiveness because this may correspond with such features as light seeds (which facilitate a species spreading), a short minimum generation time and a relatively high growth rate of seedlings, etc. (Rejmánek and Richardson 1996; Grotkopp et al. 2002; Rejmánek et al. 2005).

As was described above, there are different approaches for investigating the connections between ploidy levels and invasiveness. Some studies are focused on related invasive and non-invasive species, and others on the different species represented in a given area. In addition, a global approach is possible as was presented in the paper of Pandit et al. (2011), who collected and analyzed data for thousands of taxa from around the world.

Our study concerns the invasive and non-invasive taxa in Polish flora. Poland is a Central European country with a temperate climate. Its territory is mainly covered by plains (~90 %) without any natural barriers that could hinder plant migrations on the east–west axis. During the Pleistocene, almost the entire area of the country was covered by a glacier and therefore Polish flora is relatively young and was formed mainly in the Holocene (Szafer and Zarzycki 1977). Studies done by Chytrý et al. (2009) showed that West and Central European lowland plains are regarded as highly exposed to invasions. Moreover, this traditionally agricultural country has undergone intensive industrialization in recent decades, which was accompanied by the degradation of many natural habitats. Urban, industrial and degraded areas are also known to be susceptible to invasions (Chytrý et al. 2009; Tokarska-Guzik et al. 2011). These features make Polish flora an interesting and important area for studies on alien plant settlements and invasions, and it has therefore become the subject of many studies and data collections (INC PAS 2009; Tokarska-Guzik et al. 2012).

The main subject of our research was to investigate whether such features as chromosome numbers and polyploid frequencies are correlated with a plant's origin (native vs. alien) and invasiveness. Our previous studies (Gacek et al. 2011) proved that polyploidy is more common among indigenous plants in Polish flora. In this paper, we present more detailed results because the comparisons were done on different levels: in all angiosperms and in dicots and monocots separately. In addition, invasive and non-invasive plants were compared in the entire dataset and in alien species only. The results obtained for Polish plants may be compared to those obtained for the nuclear DNA content in the flora of our neighbor, the Czech Republic (Kubešová et al. 2010). The problems that were considered in both studies are similar, but different methods were applied and different features of genomes were compared. So our approach may shed a different light on the problem of the influence of genome parameters on the naturalization and invasiveness of plants.

Materials and methods

Data sources

Chromosome numbers were obtained mainly from the "Chromosome Number Database" (Góralski et al. 2009), which contains all of the known chromosome numbers for Polish angiosperms. In cases where the chromosome number was not known from Poland, it was acquired from other sources: Index to Plant Chromosome Numbers (Goldblatt and Johnson 1979), Karyological database of the ferns and flowering plants of Slovakia (Marhold et al. 2012), Chromosome numbers for the Italian flora (Bedini et al. 2010), the database of the Botanical Society of the British Isles (BSBI), BIOLFLOR—Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland (Klotz et al. 2002) and Mòdul Flora i Vegetació. Banc de Dades de Biodiversitat de Catalunya (Simon and Blanché 2012).

For all of the comparisons, angiosperm families that belonged to monocots and core eudicots (later named "dicots") with alien and native species were chosen. For comparisons of invasive and non-invasive species, only families with both invasive and non-invasive plants were used. We also rejected one cytotype that achieved over 100 chromosomes from the calculations.

Only cytotypes from Poland were used for the non-invasive species, while an algorithm was used for invasive species:

1. If cytotypes from Poland were known only these were used.
2. If cytotypes from Poland were not known, cytotypes from the closest geographical origin were used. The closest origin was chosen from places in the following order: neighbor countries (Germany, the Czech

Republic, Slovakia, Ukraine, Byelorussia, Russia and the countries of the former Soviet Union), other European countries and the rest of the world.

Also, for some additional comparisons, only cytotypes from Poland were used (indicated in the text).

Known x values for species were obtained mainly from: Darlington and Janaki Ammal (1945), Darlington and Wylie (1955), Holub et al. (1971), Dobes and Vitek (2000) and Klotz et al. (2002).

If x was not known for a given species, it was calculated using an algorithm:

1. If no x value is known for genera:
   a. If there is a series of $2n$ values that are multiples of an integer, this number was used as x.
   b. In other cases, the species was not used in calculations.
2. If many x numbers were known for a genera and among them was a number that is a divisor for the $2n$ of a given species, this x was used.
3. If there were $2n$ values that did not have divisors between the known x's then:
   a. If only one x was known for a genus, this one was used.
   b. If there were many x values, the closest value was used with the exception of those x values that would have meant that the $2n$ was haploid number.
   c. If the above did not provide a clear answer, the highest x for a genus was used.

The Alien Species in Poland (INC PAS 2009) database was used as the source of invasive and alien plants in Poland. A species was regarded as invasive when it was described as invasive or post-invasive. All alien species used in the study along with the status of their invasiveness are listed in Table 1.

Comparisons and groups tested

Two types of comparisons between groups were applied: chromosome numbers and polyploid frequency. Three methods were used for ploidy classification. Two were the threshold methods with the values $n \geq 11$ (Goldblatt 1980) and $n \geq 14$ (Grant 1981). The third was the modified method described by Wood et al. (2009) and referred to later as the "3.5 x method". In this case, 3.5 x values were counted for cytotypes using x values ordered to cytotypes as described above and those for which the $2n$ achieved a 3.5 of x value or more were counted as polyploids.

Tests were performed on all angiosperms and two of its classes: monocots and dicots. These classes were compared

Table 1 Alien species

Species	Invasiveness	2*n*
Acer ginnala	−	26
Acer negundo	+	26
Acer saccharinum	−	52
Achillea crithmifolia et	−	36
Acorus calamus	+	36
Aesculus hippocastanum	−	40
Agropyron cristatum	−	14
Agrostemma githago	−	48
Amaranthus bouchonii	−	32
Amaranthus chlorostachys	−	32
Amaranthus lividus	−	34
Amaranthus retroflexus	−	34
Ambrosia artemisiifolia	+	36
Anagallis arvensis forma arvensis	−	40
Anagallis foemina	−	40
Anethum graveolens	−	22
Anthemis cotula	−	18
Anthoxanthum aristatum	−	10
Apera spica-venti	−	14
Aphanes arvensis	−	48
Aphanes microcarpa	−	16
Armoracia rusticana	−	32
Artemisia abrotanum	−	18, 36
Artemisia annua	−	18
Artemisia austriaca	−	16
Artemisia dracunculus	−	90
Asclepias cornuti	−	22
Aster lanceolatus	+	64
Aster novae-angliae	+	10
Aster novi-belgii	+	54
Aster tradescantii	+	16
Atriplex hortensis	−	18
Atriplex nitens	−	18
Atriplex tatarica	−	18
Avena fatua	−	42
Avena sativa	−	42
Ballota nigra	−	22, 20
Barbarea intermedia	−	16
Bidens frondosa	+	48
Borago officinalis	−	16
Brassica elongata	−	22
Bromus arvensis	−	14
Bromus carinatus et	−	56
Bromus secalinus	−	28
Bromus sterilis	−	14
Bromus tectorum	−	14
Bromus willdenowii	−	42
Bunias orientalis	+	14

Table 1 continued

Species	Invasiveness	2*n*
Calendula officinalis	−	32
Camelina rumelica	−	12
Camelina sativa	−	40
Cannabis sativa	−	20
Capsella bursa-pastoris	−	32
Caragana arborescens	−	16
Carduus acanthoides	−	22
Carduus nutans	−	16
Centaurea cyanus	−	24
Chamomilla recutita	−	18
Chamomilla suaveolens	−	18
Chenopodium aristatum	−	18
Chenopodium bonus-henricus	−	36
Chenopodium ficifolium	−	18
Chenopodium hybridum	−	18
Chenopodium murale	−	18
Chenopodium suecicum	−	18
Chrysanthemum segetum	−	18
Cichorium intybus	−	18
Clematis vitalba	+	16
Consolida regalis	−	16
Conyza canadensis	−	18
Corispermum hyssopifolium	−	18
Corispermum nitidum	−	18
Cornus mas	−	18
Cornus sericea	+	22
Crepis aurea	+	10
Crocus vernus	−	16
Cymbalaria muralis	−	14
Datura stramonium	−	24
Descurainia sophia	−	28
Digitaria sanguinalis	−	36
Diplotaxis muralis	−	42
Echinacea purpurea	−	22
Echinochloa crus-galli	+	54
Echinops commutatus	−	30
Echinops sphaerocephalus	+	30, 32
Elaeagnus angustifolia	−	28
Elaeagnus commutata	−	28
Elodea canadensis	+	48
Elodea nuttallii	−	48
Elsholtzia ciliata	−	16
Epilobium adenocaulon	−	36
Eragrostis pilosa	+	20
Erigeron annuus	−	27
Eruca vesicaria subsp. sativa	−	22
Euphorbia exigua	−	16, 24
Euphorbia helioscopia	−	42

Table 1 continued

Species	Invasiveness	2*n*
Euphorbia peplus	−	16
Fagopyrum esculentum	−	16
Fagopyrum tataricum	−	16
Fallopia convolvulus	−	40
Fraxinus pennsylvanica	−	46
Galinsoga parviflora	−	16
Galinsoga quadriradiata	−	32
Geranium dissectum	−	22
Geranium divaricatum	−	28
Geranium molle	−	26
Geranium pusillum	−	26
Geranium pyrenaicum	−	26, 28
Geranium sibiricum	−	28
Glaucium flavum	−	12
Gleditsia triacanthos	−	28
Helianthus annuus	−	34
Helianthus decapetalus	−	34
Helianthus tuberosus	+	102
Helianthus x laetiflorus	−	102
Heracleum mantegazzianum	+	22
Heracleum sosnovskii	+	22
Herniaria hirsuta	−	36
Hesperis matronalis	−	24
Hordeum murinum	−	28
Humulus scandens	−	16, 17
Hyoscyamus niger	−	34
Impatiens capensis	+	20
Impatiens parviflora	+	26
Impatiens roylei	+	18
Inula helenium	−	20
Iva xanthifolia	−	36
Juncus tenuis	−	40
Kochia scoparia	−	18
Lactuca serriola	−	18
Lamium album	−	18
Lamium amplexicaule	−	18
Lamium purpureum	−	18
Lathyrus tuberosus	−	14
Leonurus cardiaca	−	18
Lepidium campestre	−	16
Lepidium densiflorum	−	32
Lepidium latifolium	−	24
Lepidium perfoliatum	−	16
Lepidium ruderale	−	32
Lepidium sativum	−	24
Lepidium virginicum	−	32
Levisticum officinale	−	22
Linum austriacum	−	18

Table 1 continued

Species	Invasiveness	2*n*
Linum perenne	−	18
Linum usitatissimum	−	30
Lithospermum arvense	−	28
Lolium multiflorum	+	14
Lolium remotum	−	14
Lupinus angustifolius	−	40
Lupinus luteus	−	52
Lupinus polyphyllus	−	48
Lychnis coronaria	−	24
Lycium halimifolium	−	48, 24
Malope trifida	−	44
Malva alcea	−	84
Malva crispa	−	120, 112
Malva moschata	−	42
Malva neglecta	−	42
Malva pusilla	−	42
Malva silvestris	−	42
Malva verticillata	−	84
Marrubium vulgare	−	34
Matricaria maritima	−	18, 36
Medicago sativa	+	32
Melandrium noctiflorum	−	24
Mentha rotundifolia	−	54
Mentha x gentilis (= spicata x arvensis)	−	60
Mercurialis annua	−	16
Mimulus guttatus	+	28
Mimulus moschatus	+	32
Misopates orontium	−	16
Myosotis arvensis	−	52
Myrrhis odorata	+	22
Nepeta cataria	−	36
Nigella arvensis	−	12
Oenothera acutifolia	−	14
Oenothera albipercurva	−	14
Oenothera fallax	−	14
Oenothera glazioviana	−	14
Oenothera hoelscheri	−	14
Oenothera issleri	−	14
Oenothera jueterborgensis	−	14
Oenothera paradoxa	−	14
Oenothera parviflora	−	14
Oenothera pseudochicaginensis	−	14
Oenothera pycnocarpa	−	14
Oenothera renneri	−	14
Oenothera salicifolia	−	14
Oenothera silesiaca	−	14
Oenothera suaveolens	−	14
Oenothera syrticola	−	14

Table 1 continued

Species	Invasiveness	2*n*
Oenothera turoviensis	−	14
Oenothera vratislaviensis	−	14
Oenothera wienii	−	14
Onobrychis viciifolia	+	28
Onopordum acanthium	−	34
Ornithogalum nutans	−	42
Oxalis stricta	−	24
Oxycoccus macrocarpus	−	24
Padus serotina	+	32
Panicum miliaceum	−	36
Parietaria officinalis	−	14
Petroselinum crispum	−	22
Phalaris canariensis	−	12
Phleum rhaeticum	−	14
Physalis alkekengi	−	24
Physocarpus opulifolius	−	18
Pimpinella anisum	−	20
Polygonum orientale	−	22
Potentilla intermedia	−	56
Quercus cerris	+	24
Quercus rubra	−	24
Raphanus raphanistrum	−	18
Raphanus sativus	−	18
Reynoutria japonica	+	88
Reynoutria sachalinensis	+	44, 66, 88
Reynoutria x bohemica	+	66, 44, 88
Robinia pseudacacia	+	20
Rosa blanda	−	14
Rosa glauca	−	28
Rosa pimpinellifolia	−	28
Rosa rugosa	−	14
Rubus odoratus	−	14
Rubus xanthocarpus	−	14
Rudbeckia hirta	−	38
Rudbeckia laciniata	−	76, 38
Rumex confertus	−	60
Scleranthus annuus	−	44
Scorzonera hispanica	−	14
Scrophularia vernalis	−	40
Senecio inaequidens	+	40
Senecio vulgaris	−	40
Setaria glauca	−	36
Setaria italica	−	18
Sherardia arvensis	−	22
Silene dichotoma	−	24
Silybum marianum	−	34
Sinapis alba	−	24
Sinapis arvensis	−	18

Table 1 continued

Species	Invasiveness	2*n*
Sisymbrium loeselii	−	14
Sisymbrium officinale	−	14
Solanum nigrum	−	72
Solidago canadensis	+	18
Solidago gigantea	+	36
Sonchus asper	−	18
Sonchus oleraceus	−	36
Spergula arvensis	−	18
Symphoricarpos albus	+	54
Symphyotrichum ciliatum	−	14
Syringa josikaea	−	44
Syringa vulgaris	−	44
Thlaspi arvense	−	14
Trifolium patens	−	14
Trifolium resupinatum	−	16
Trigonella coerulea	−	16
Urtica cannabina	−	52
Urtica urens	−	24
Veronica arvensis	−	16
Veronica filiformis	−	14
Veronica persica	−	28
Veronica polita	−	14
Veronica triphyllos	−	14
Vicia dasycarpa	−	14
Vicia grandiflora	−	14
Vicia hirsuta	−	14
Vicia sativa	−	12
Vicia tetrasperma	−	14
Vicia villosa	−	14
Viola arvensis	−	34
Vitis vinifera	−	38
Xanthium albinum	+	36
Xanthium spinosum	−	36
Xanthium strumarium	−	36

as being non-invasive to invasive and native to alien species in angiosperms and in both classes.

Statistics tools and procedures

All of the analyses and graphs were done in the R environment for statistical computing (R Development Core Team 2012). For testing differences between chromosome numbers in groups, the non-parametric Mann–Whitney *U* (Wilcoxon) test was used (wilcox.test function from the stats library). Diploid and polyploid frequencies and frequencies of invasive plants in the groups studied were compared using the Pearson's χ^2 test for small samples, those containing fewer than ten cytotypes and the results of χ^2 test with the Yates correction for small samples (chisq.test from stats library). Confidence intervals were calculated using the test of equal or given proportions (prop.test from stats library).

Results

Chromosome numbers

The results of the most important statistical tests are presented in Tables 2 and 3. Table 2 contains the results for the chromosome numbers of invasive and non-invasive taxa in angiosperms, dicots and monocots as well as comparisons of native and alien taxa. The results of the comparisons of the diploid and polyploid fractions in these groups are presented in Table 3.

In total, 1,428 cytotypes were investigated. Chromosome numbers ranged from 6 to 96. The most frequent chromosome number (mode) was 28. Chromosome number frequencies are displayed in Fig. 1.

Forty-two of the cytotypes investigated belonged to invasive species (4.3 %) and 927 to non-invasive species (95.7 %). The minimum, mean and median values of the 2*n* were higher for invasive angiosperms than for non-invasive ones (Table 2). The mean 2*n* value for the first group was more than six chromosomes higher, whereas the median difference was smaller (4). The Mann–Whitney test indicated that the difference between groups is statistically significant ($p < 0.05$). Generally, all of the parameters that were checked were the same or almost the same for non-invasive angiosperms and for all of the native angiosperms that were tested. Chromosome number distributions for both groups are shown in Fig. 2b.

Most of the plants studied were dicots (81.7 %). Comparisons of monocots and dicots showed that the mode and median were equal and was the same for both groups (28). Monocots had a higher mean (32.5 vs. 30.8) but the statistical test did not prove that the difference is statistically significant ($p = 0.39$). The span of 2*n* numbers was wider in dicots (6–96) than in monocots (10–94). The parameters for Polish-only cytotypes were nearly the same.

The almost twofold difference in the frequency of invasive plants in dicots (4.8 %) and in monocots (2.6 %) was found not to be statistically significant ($p = 0.18$). Invasive plants had a higher mean chromosome number than non-invasive ones in the case of dicots (36.6 vs. 29.0) and monocots; however, in the latter it was less significant (34.4 vs. 33.4). Higher medians were also noted for invasive plants than for non-invasive ones in both dicots (32 vs. 28) and monocots (36 vs. 28). The Mann–Whitney test

Table 2 Statistical comparison of the groups studied

Cytotypes	Number of cytotypes	Chromosome numbers (2*n*)					Mann–Whitney test (*p*)
		Min.	Max.	Mean (SD)	Mode (number)	Median	
Angiosperms	1,428	6	96	31.1 (16.5)	28 (167)	28	–
Angiosperms non-invasive	927	6	96	29.9 (15.6)	28 (137)	28	<0.05
Angiosperms invasive	42	10	88	36.4 (20.7)	22, 32, 36 (4)	32	
Angiosperms native	1,020	6	96	31.9 (16.6)	28 (139)	28	<0.05
Angiosperms alien	275	10	90	27.9 (15.6)	14 (48)	24	
Angiosperms alien non-invasive	128	10	90	25.7 (13.5)	14 (26)	22	<0.05
Angiosperms alien invasive	42	10	88	36.4 (20.7)	22, 32, 36 (4)	32	
Dicots	1,166	6	96	30.8 (16.1)	28 (113)	28	0.39
Monocots	262	10	94	32.5 (17.8)	28 (54)	28	
Dicots non-invasive	738	6	96	29,0 (14.5)	28 (89)	28	<0.05
Dicots invasive	37	10	88	36.6 (21.3)	32 (4)	32	
Dicots native	814	6	96	31.5 (16.1)	28 (95)	28	<0.05
Dicots alien	247	10	90	27.8 (15.7)	14 (40)	22	
Dicots alien non-invasive	108	12	90	25.5 (13.3)	14 (19)	22	<0.05
Dicots alien invasive	37	10	88	36.6 (21.3)	22, 32 (4)	32	
Monocots non-invasive	189	10	94	33.4 (19.0)	28 (48)	28	0.74
Monocots invasive	5	14	54	34.4 (17.3)	–	36	
Monocots native	206	10	94	33.2 (18.6)	28 (44)	28	0.29
Monocots alien	28	10	56	28.6 (14.8)	14 (8)	28	
Monocots alien non-invasive	10	10	18	13.8 (2.0)	14	7	0.05
Monocots alien invasive	3	14	36	23 (11.4)	–	20	

proved that these differences were statistically significant only for dicots ($p < 0.05$). The most frequent chromosome number in dicots was higher in invasive plants (32 vs. 28) (Fig. 2d). The medians for invasive monocots are not shown because all five cytotypes had different 2*n* values.

Among the 1,295 cytotypes, 78.8 % belonged to native species and 21.2 % to alien species. Statistical comparisons of the 2*n* values showed that plants from the latter group have a lower mean (27.9 vs. 31.9), mode (14 vs. 28) and median (22 vs 24) (Table 2; Fig. 2a). The difference in the chromosome numbers between these groups was significant ($p < 0.05$). Similar tendencies were observed in dicots, where the parameters mentioned above had the same or almost the same values, except for the median for alien dicots, which was two chromosomes lower ($p < 0.05$) (Table 2; Fig. 2c). The results obtained for monocots displayed similar tendencies. The mean (28.6 vs. 33.2) and mode (14 vs. 28) were lower in alien species than in native ones, but the medians were the same (28) and the difference was not statistically significant ($p = 0.29$) (Table 2).

Chromosome numbers in the group of alien species were compared between invasive and non-invasive plants. In alien angiosperms, invasive species had a higher mean (36.4 vs. 25.7), modes (22, 32 and 36 vs. 14) and median (32 vs. 22) than non-invasive ones and according to the Mann–Whitney result, the difference was statistically significant ($p < 0.05$). Similar differences were observed in the group of alien dicots ($p < 0.05$). The group of alien monocots, especially invasive plants, was too small to draw any reliable statistical conclusions.

Polyploid frequencies

Polyploid frequencies were examined in the same groups of species as above. In order to estimate the number of polyploids, two threshold methods ($n \geq 11$ and $n \geq 14$) and the 3.5 *x* method were used. The results of these comparisons are shown in Table 3; Figs. 3, 4, 5.

The highest polyploid frequencies in almost all of the groups tested were generally noted for the $n \geq 11$ threshold, rather than for the $n \geq 14$ threshold and the lowest were noted for the 3.5 *x* method. The exceptions are some groups of monocots that had equal results for some or all of the methods. When all of the alien monocots were examined using all three methods, the proportions between diploids and polyploids were the same (44.4–55.6 %); in the within-group (alien non-invasive and invasive monocots), the probes were too small to draw any reliable statistical conclusions and therefore they were omitted from later considerations.

Table 3 Ploidy in the groups studied

	3.5 *x* method			Threshold 11			Threshold 14		
	Diploids (%)	Polyploids (%)	χ^2 test (*p*)	Diploids (%)	Polyploids (%)	χ^2 test (*p*)	Diploids (%)	Polyploids (%)	χ^2 test (*p*)
Angiosperms	705 (49.7)	714 (50.3)	–	453 (31.7)	975 (68.3)	–	652 (45.7)	776 (54.3)	–
Angiosperms non-invasive	466 (50.6)	455 (49.4)	0.94	316 (34.1)	611 (65.9)	0.17	431 (46.5)	496 (53.5)	0.44
Angiosperms invasive	21 (50.0)	21 (50.0)		10 (23.8)	32 (76.2)		17 (40.5)	25 (59.5)	
Angiosperms native	473 (46.4)	547 (53.6)	<0.05	296 (29.0)	724 (71.0)	<0.05	438 (42.9)	582 (57.1)	<0.05
Angiosperms alien	176 (64.0)	99 (36.0)		121 (44.0)	154 (56.0)		161 (58.5)	114 (41.5)	
Angiosperms alien non-invasive	85 (66.4)	43 (33.6)	0.09	63 (49.2)	65 (50.8)	<0.05	79 (61.7)	49 (38.3)	<0.05
Angiosperms alien invasive	21 (50.0)	21 (50.0)		10 (23.8)	32 (76.2)		17 (40.5)	25 (59.5)	
Dicots	604 (52.2)	554 (47.8)	<0.05	267 (34.5)	508 (65.5)	0.28	378 (48.8)	397 (51.2)	<0.05
Monocots	101 (38.7)	160 (61.3)		59 (40.4)	135 (69.6)		70 (36.1)	124 (63.9)	
Dicots non-invasive	399 (54.4)	334 (45.6)	0.49	259 (35.1)	479 (64.9)	0.13*	363 (47.6)	375 (52.4)	0.30
Dicots invasive	18 (48.6)	19 (51.4)		8 (21.6)	29 (78.4)		15 (40.5)	22 (59.5)	
Dicots native	393 (48.3)	421 (51.7)	<0.05	234 (28.7)	580 (71.3)	<0.05	358 (44.0)	456 (56.0)	<0.05
Dicots alien	163 (66.0)	84 (34.0)		108 (43.7)	139 (56.3)		148 (59.9)	99 (40.1)	
Dicots alien non-invasive	75 (69.4)	33 (30.6)	<0.05	53 (49.1)	55 (50.9)	<0.05*	69 (63.9)	39 (36.1)	<0.05
Dicots alien invasive	18 (48.6)	19 (51.4)		8 (21.6)	29 (78.4)		15 (40.5)	22 (59.5)	
Monocots non-invasive	67 (37.2)	113 (62.8)	0.57*	57 (30.2)	132 (69.8)	1.00*	68 (36.0)	121 (64.0)	1.00*
Monocots invasive	3 (60.0)	2 (40.0)		2 (40.0)	3 (60.0)		2 (40.0)	3 (60.0)	
Monocots native	80 (38.8)	126 (61.2)	0.44	62 (30.1)	144 (69.9)	0.08	80 (38.8)	126 (61.2)	0.58
Monocots alien	13 (46.4)	15 (53.6)		13 (46.4)	15 (53.6)		13 (46.4)	15 (53.6)	
Monocots alien non-invasive	10 (100)	0 (0)	–	10 (100)	0 (0)	0.51*	10 (100)	0 (0)	0.35*
Monocots alien invasive	3 (100)	0 (0)		2 (66.7)	1 (33.3)		2 (66.7)	1 (33.3)	

* Test with Yates correction

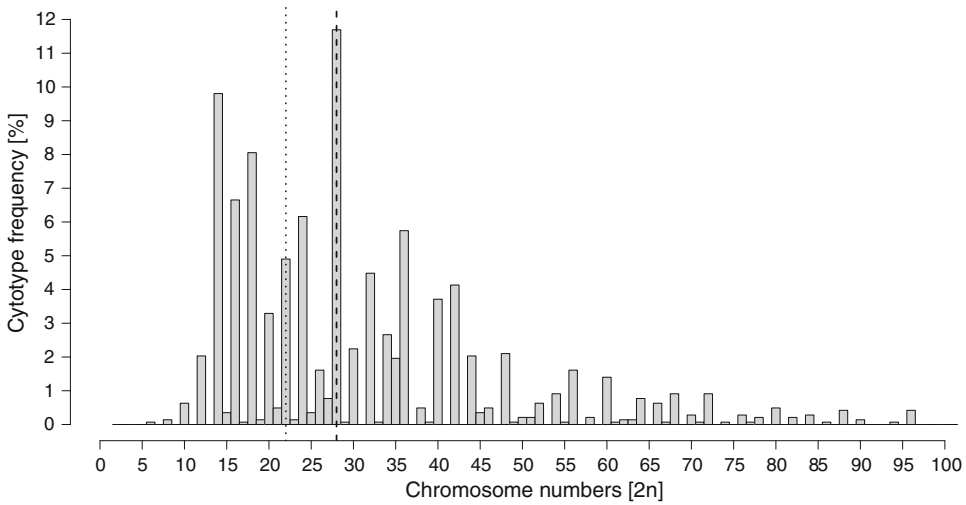

Fig. 1 Distribution of chromosome numbers in angiosperms. *Vertical lines* indicate polyploidy thresholds for the 2*n* values: $n = 11$ (*dotted line*) and $n = 14$ (*dashed line*)

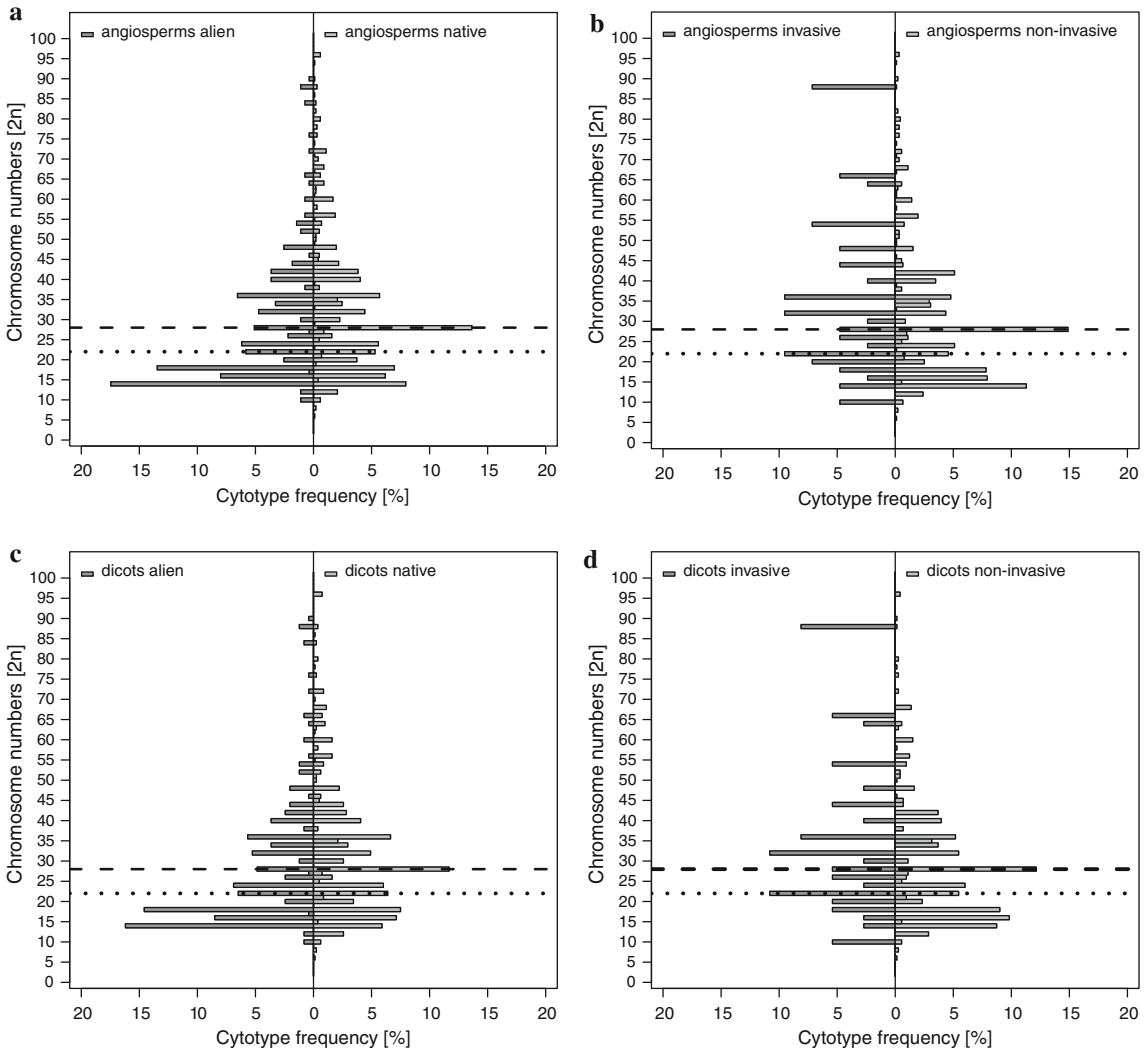

Fig. 2 Frequencies of cytotypes in some of the groups studied. Pairs of datasets compared: **a** alien and native angiosperms, **b** invasive and non-invasive angiosperms, **c** alien and native dicots, **d** invasive and non-invasive dicots. *Horizontal lines* indicate polyploidy thresholds for the 2*n* values: $n = 11$ (*dotted line*) and $n = 14$ (*dashed line*)

Two classes of angiosperms differ in the abundance of polyploids. Monocots have about 1.5–13.9 % more polyploid cytotypes than dicots, but the difference is statistically insignificant for the $n \geq 11$ threshold ($p = 0.28$). Comparisons of polyploid frequencies between non-invasive and invasive species showed that in most cases (except for most of the methods for monocots), they were higher in the cytotypes of invasive plants and that these differences were statistically significant ($p < 0.05$) for alien angiosperms (except for the 3.5 *x* method) and alien dicots.

When native and alien taxa were compared, the χ^2 test proved that the differences were statistically significant ($p < 0.05$), with the exception of the comparisons of monocots. In the rest of the groups tested (angiosperms, dicots) and for all three methods that were used to estimate the frequency of polyploids, alien plants generally had a lower fraction of polyploids than native ones.

Discussion

Because a plant invasion is preceded by the process of naturalization (Richardson and Pyšek 2006; Williamson 2006; Pyšek et al. 2008), the features that enable plants to survive and establish a stable population in a new area are important for their ability to invade and prosper. One such feature is genome size, although there are two opposite processes that can be regarded as promoting plant naturalization and invasiveness. The first is the process of polyploidization, which may support a plant through benefits that have been described by many authors and that were briefly summarized in the introduction of this paper. Polyploidization, which is the process of genome multiplication, results in genomes with a higher DNA content and higher chromosome numbers. The second process is the loss of genetic material, which may also be beneficial,

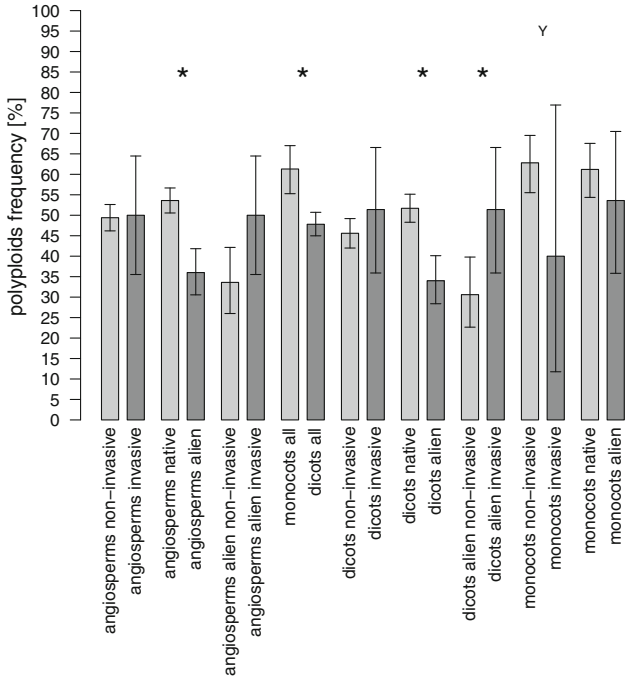

Fig. 3 Polyploid frequencies for the 3.5 *x* method. *Error bars* indicate confidence intervals, *dashed line* with Yates correction, *solid line* without Yates correction. *Asterisks* indicate pairs with a significant difference

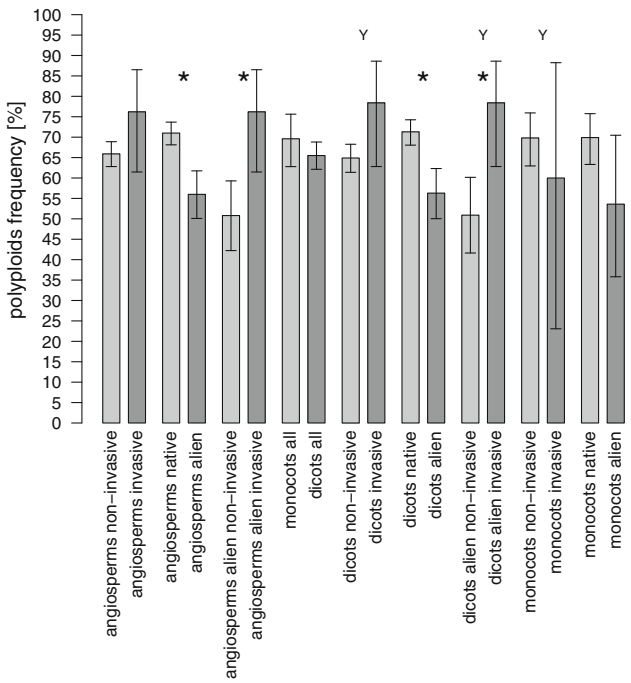

Fig. 4 Polyploid frequency in the groups studied (threshold $n \geq 11$). *Error bars* indicate confidence intervals, *dashed line* with Yates correction, *solid line* without Yates correction. *Asterisks* indicate pairs with a significant difference

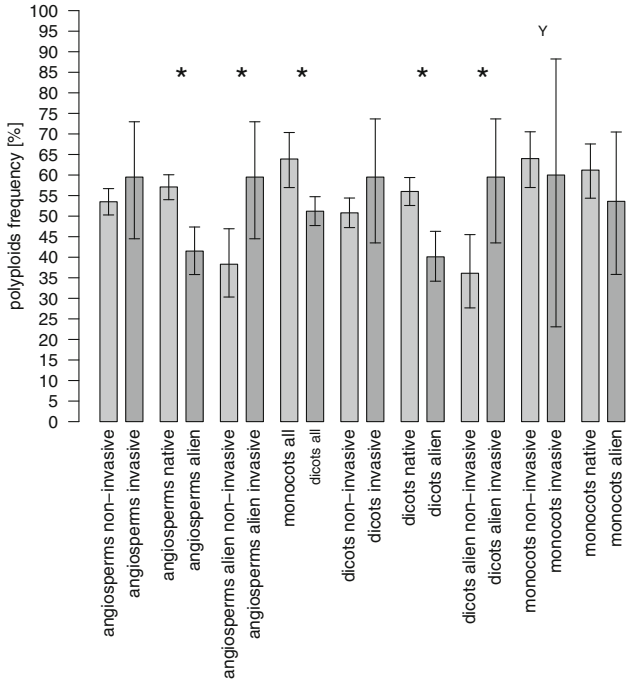

Fig. 5 Polyploid frequency in the groups studied (threshold $n \geq 14$). *Error bars* indicate confidence intervals, *dashed line* with Yates correction, *solid line* without Yates correction. *Asterisks* indicate pairs with a significant difference

e.g., by shortening the life cycle and making it possible to produce numerous light seeds, etc. (Rejmánek and Richardson 1996; Rejmánek et al. 2005; Grotkopp et al. 2002). Because these two processes have an opposite effect on genomes, depending on which of them is more influential, one may suspect that alien species have larger or smaller genomes.

The results presented here showed significant differences in both chromosome numbers and polyploid frequencies between alien and native species in most cases. Generally, aliens had fewer chromosome numbers and fewer polyploid frequencies than native plants. The one exception was the comparison of the group of monocots, for which such differences were not statistically significant. These observations are in accordance with our previous karyological analysis of Polish flora (Gacek et al. 2011) and also correspond with studies on genome size in native and alien species of the Czech Republic that was done by Kubešová et al. (2010). However, it is difficult to directly compare results obtained by such different methods. Due to differences in chromosome size, plants with a similar nuclear DNA content may differ in chromosome number and vice versa (Bennett 1987; Bailey and Stace 1992; Joachimiak et al. 2001; Johnston et al. 2005; Greilhuber et al. 2008; Klos et al. 2009).

It would be interesting to obtain data on variations in chromosome numbers in native and alien plant species from other countries/geographical areas. It is known that different flora show different distributions of chromosome numbers (Peruzzi et al. 2011, 2012), but little is known about the possible differences between indigenous and non-indigenous plants within them.

The results obtained in this study suggest a tendency of alien plants to have lower chromosome numbers and a lower proportion of polyploids, although it could be argued that this may be caused by unequal distributions of alien plants between taxa, which might differ by chromosome number or for some reasons other than invasiveness. This seems to be especially important when two classes of angiosperms are considered because chromosome number distributions are different in phylogenetic groups (Bedini et al. 2012a, b). In addition, these classes differ in the frequencies of growth forms and it is believed that the frequency of polyploids differs among them (Stebbins 1971; Levin and Wilson 1976; te Beest et al. 2012). For these reasons, not only data of families that had no alien species were removed, but also within-class comparisons were performed. The differences between native and alien plants proved to be statistically significant only in dicots. The differences were not statistically significant in less numerous monocots, although the estimates showed a higher proportion of polyploids among native plants. One of the possible explanations for the generally lower chromosome numbers in aliens may be changes in respect to latitude. Recently, analyses of flora in Italy, Slovakia and Poland showed that polyploid frequency increases proportionally with distance from the Equator (Peruzzi et al. 2012). This observation may explain why non-indigenous plants in Poland that originated mainly in the south have fewer chromosomes than native species.

The idea that polyploidy affects invasiveness, however popular, has rarely been supported by broader research. One of the exceptions was an analysis of the relationship between ploidy and invasiveness in worldwide flora done by (Pandit et al. 2011) as it concerned taxa from very different geographical regions, evolutionary histories and climatic conditions. The studies of plants in Singapore, although much narrower, were also interesting (Pandit et al. 2006). Our study focused on the flora of one country with conditions that are not very differentiated, so any climatically, geographically and historically determined differences within it are not large. On the other hand, Polish flora seems to be rich enough to make some wider observations and to draw more general conclusions.

The cytotypes of invasive species shared only a small part of all of the data that was studied (ca. 4.3 %). The distribution of chromosome numbers between invasive and non-invasive plants showed higher values of the mean, mode and median for the first group. These differences were statistically significant for angiosperms and for dicots, including the test for alien dicots, but not for monocots. The corresponding tests for polyploid frequency showed similar tendencies, but were statistically significant only for alien dicots for three methods.

Our results did prove that in most of the groups that were studied, invasiveness is correlated with an increase in chromosome number as was reported in some other studies (Lowry and Lester 2006; Pandit et al. 2006, 2011; te Beest et al. 2012). Although alien plants showed generally lower numbers than native species, the invasive ones have more chromosomes than the non-invasive ones. This may suggest that a lower chromosome number is advantageous for plant naturalization, but not for becoming an invasive species. Kubešová et al. (2010) came to similar conclusions in relation to the amount of nuclear DNA in invasive and non-invasive species of alien flora in the Czech Republic. The authors suggested that small genomes are advantageous in the naturalization stage, but do not necessarily play a role in the next stage when naturalized plants become invasive. According to these authors, "a small genome size provides alien plants with an advantage already at the stage of naturalization and need not necessarily be associated with the final stage of the process, i.e. invasion". Our results may suggest that invasive species recruited from those aliens had higher chromosome numbers from the beginning or that they increased their chromosome number after naturalization. In the latter case, it is conceivable that the transition into the invasive stage requires a genetic enhancement by polyploidization or at least by gaining additional chromosomes through aneuploidization.

It is also noticeable that the differences in chromosome numbers of native and alien species and for invasive and non-invasive plants are statistically significant for dicots, but not for monocots. The number of data for monocots is smaller than for dicots, especially in the case of invasive species (only five cytotypes), which affects the strength of statistical tests. However, it should be mentioned that the difference of the mean $2n$ values between invasive and non-invasive monocots (1) is very small and that the p value calculated by the Mann–Whitney test is relatively high (0.74). This may suggest that other factors, such as the dominating life-forms of monocots or taxonomical reasons may cause changes in chromosome numbers that are not as important in the case of monocots as in dicots, especially for the phenomenon of invasiveness.

In our opinion, our results enrich the knowledge about correlations of changes in chromosome numbers with such processes as the settlement of alien species and their invasiveness, but also indicate that further studies in these areas are needed. For example, larger datasets, especially

for alien and invasive plants, would make the results more reliable and that comparisons of cytotypes of alien/invasive plants found in Poland with their counterparts in the countries from which they originated may also shed some light on the problems discussed here.

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